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Reproductive Hormone Profiles in Captive Male Orangutans: Implications for Understanding Developmental Arrest

ANNE N. MAGGIONCALDA,[1]* ROBERT M. SAPOLSKY, [2]
AND NANCY M. CZEKALA[3]
[1]*Department of Anthropological Sciences, Stanford University, Stanford, California 94305-2145*
[2]*Department of Biological Sciences, Stanford University, Stanford, California 94305-5020*
[3]*Center for Reproduction of Endangered Species, Zoological Society of San Diego, San Diego, California 92112-0551*

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ABSTRACT For many years researchers have described some male orangutans as "subadult." These males are of adolescent to adult age and are reproductive, but have little to no secondary sexual trait development. Until now the only endocrine study of this arrest of secondary sexual trait development was performed by Kingsley (1982, 1988). She found that "subadult" or arrested males have lower testosterone levels than similar age developing adolescents or adult males. In this study, urine samples were collected over a two-year period from 23 captive male orangutans in order to more fully define male endocrine profiles. Three study males were juveniles, seven were arrested adolescents, six were developing adolescents, and seven were mature adults. Morning samples were analyzed by radioimmunoassay for levels of testicular steroids and gonadotropins and group hormone profiles were compared by analysis of variance. Results illustrate that arrested adolescent orangutans have significantly lower testosterone and dihydrotestosterone (DHT) levels than developing adolescents, but significantly higher levels than juveniles. Luteinizing hormone (LH) levels also differed between arrested and developing adolescents, with arrested males having lower levels. However, follicle stimulating hormone (FSH) levels were similar in both morphs of adolescent male. The overall hormone profiles for arrested and developing adolescent male orangutans suggest that arrested males lack levels of LH, testosterone, and DHT necessary for development of secondary sexual traits. However, they have sufficient testicular steroids, LH, and FSH to fully develop primary sexual function and fertility. These endocrine data help define alternative developmental pathways in male orangutans. The authors discuss the relationship between these developmental pathways and male orangutan reproductive strategies, and hypothesize about their prepubertal socioendocrine determination. Am J Phys Anthropol 109:19–32, 1999.

Among both captive and wild orangutans, two morphs of reproductive male are observed, namely those with secondary sexual features and those without (Kingsley, 1982; te Boekhorst et al., 1990). Orangutans have the most variable timing of maturation among the apes. In males, maturation in-

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*Correspondence to: Anne N. Maggioncalda, Department of Anthropological Sciences, Stanford University, Stanford, CA 94305-2145. E-mail: anmagg@hotmail.com

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cludes not only gonadal maturation and fertility onset, but also development of marked secondary sexual features, such as cheek flanges, laryngeal sac, beard and mustache, large body size, and a musky odor (Graham and Nadler, 1990). In captivity, puberty typically occurs between the ages of 7 and 9 years, but may occur as early as 5 or as late as 16. Commonly males are fully mature by 14, but some males may look immature or subadult for years longer. Both in captivity and the wild, maturation can be very rapid or take many years. Wild males may stay subadult for 10 or more years, an estimated 50 to 605 of their reproductive life span (te Boekhorst et al., 1990).

Males with secondary sexual features typically exhibit at least two mating strategies: a male may maintain a range and mate with resident females, or may be nomadic, mating opportunistically in other males' ranges (Galdikas, 1981). These males typically consort with females, but they also force copulations (Mitani, 1985a). Likewise, males lacking secondary sexual features have at least two mating strategies: they may be tolerated by a mature, resident male and spend most of their time in his range, or may wander, in search of females and food. These subadult males may consort with females of various ages; however, most copulations between such males and reproductive females are forced (Galdikas, 1981; Mitani, 1985a).

Female orangutans do not have estrous swellings as the other great apes do, but have been reported to have marked proceptive behavior to signal their fertility (Galdikas, 1981; Nadler, 1982). Only dominant, mature males present appropriate physical signs and behaviors to elicit female proceptivity. Galdikas (1981) speculates that male secondary sexual traits signal that the male has survived to maturity and therefore has traits consistent with breeding success. Despite the apparent unattractiveness of subadult males to females, forced copulations have allowed these males to sire in captivity (Kingsley, 1982) and probably also in the wild (MacKinnon, 1974; Galdikas, 1985a, 1985b).

The decoupling of fertility and secondary sexual trait development in some male orangutans theoretically has costs and benefits for both mature males and subadult or developmentally arrested males. Mature males may have higher testosterone levels than other classes of male (Kingsley, 1982). This may incur associated costs including decreased health and life span (due to the metabolic effects, such as suppressed immunity), and higher mortality rates from intrasexual aggression and injury (McCruden and Stimson, 1991; Dufty, 1989; Ralls et al., 1980). Additionally, the mature male's large body size requires considerable energy to maintain and incurs locomotor costs given the relative difficulty of arboreal travel for them. Because secondary sexual development is arrested in subadult males, they postpone these costs. The counterbalancing benefits of full maturation are obvious: mature males are dominant to all other orangutan age and sex classes and have priority to fertile females and food sources (Utami et al., 1997). Subadult males, on the other hand, defer the costs and benefits of maturation until success is more likely, for example when a mature male ages or dies and they can replace him as a range-holder. Subadult males are fertile but inconspicuous and avoid mature males (Galdikas, 1985c). This unobtrusiveness allows them access to reproductive females and opportunities to sire offspring.

According to Maple (1980), "unwritten zoo lore" holds that "complete development of secondary sex characteristics seems to be suppressed" in young males housed with adult males. However, if the dominant male is removed, the arrested male begins to develop immediately. Graham and Nadler (1990) have also observed the arrest phenomenon in captive orangutans, and that males raised in isolation mature earlier than those housed with other males. These observations suggest that developmentally arrested male orangutans represent a socioendocrine example of social environment affecting developmental time line. Furthermore, social inconspicuousness with other males and forced copulation with females represent an alternative reproductive strategy for these males. Kingsley (1982, 1988) performed the only endocrine studies of this arrest phenom-

enon, which involves assessment of testosterone levels.

The impact of testosterone and allied hormones on males

Testosterone is a testicular steroid hormone which is responsible for human male sexual maturation, including testes and penis growth, and it facilitates spermatogenesis (Griffin and Wilson, 1992; Al-Attia et al., 1993). In numerous species, male signals of aggression are testosterone-dependent (Wingfield et al., 1994; Higley et al., 1996). Testosterone levels change over the course of the human male life span, being low in children, increasing during puberty, plateauing in adults, and possibly decreasing in aged men (Griffin and Wilson, 1992; Vom Saal et al., 1994). Dihydrotestosterone (DHT), follicle stimulating hormone (FSH), and luteinizing hormone (LH) also have central roles in human growth, development, and reproduction. Testosterone can be converted to the biopotent metabolite DHT, which functions in the development of some secondary sexual features during adolescence (Griffin and Wilson, 1992). The gonadotropins, LH and FSH, are pituitary peptide hormones secreted in response to hypothalamic gonadotropin-releasing hormone (GnRH) (Thorner et al., 1992). The primary sites of gonadotropin receptors are the gonads. Beginning at puberty, LH stimulates testosterone production and secretion and FSH stimulates spermatogenesis (Thorner et al., 1992).

Purpose of this study

In this study, we replicate Kingley's assessment of testosterone levels and also assess samples for DHT, FSH and LH. Furthermore, we define the reproductive hormone profiles of juvenile, arrested adolescent, developing adolescent, and adult male orangutans, to more fully understand the physiological mechanism of decoupling primary and secondary maturation. Additionally, we consider the evolutionary implications of paired fertility and lack of secondary sexual traits in terms of male reproductive strategies. Last, we propose that the variable timing of secondary sexual development in male orangutans is determined by prepubertal socioendocrine events.

MATERIALS AND METHODS

Subjects

Urine samples were analyzed for juvenile, arrested adolescent, developing adolescent, and fully mature adult captive male orangutans. The 23 males studied ranged in age from 3 to 26 years. Groups were based on age, degree of secondary sexual maturation as primarily measured by cheek flange and laryngeal sac development, and body size (Table 1). Three males were juveniles. They were between the ages of 3 and 5 years, with no signs of secondary sexual development. Seven males were arrested adolescents. They were at least 7 years old and showed no signs of flange or laryngeal sac development. Six males were developing adolescents. They were at least 6 years old, increasing in body weight, and in the process of developing cheek flanges and an enlarged laryngeal sac. Seven males were adults. They were fully mature, based on large flanges, enlarged laryngeal sac and stasis in body size, and between 15 and 26 years of age. Seven males studied were the Bornean subspecies, *Pongo pygmaeus pygmaeus*, eight were the Sumatran subspecies, *Pongo pygmaeus abelii*, and eight males were subspecies hybrids. The subspecies differ in hair color and facial morphology, but other physical and behavior traits appear to be similar between the two populations (Rodman and Mitani, 1987). Males were housed at Audubon Zoo, Brookfield Zoo, Chaffee Zoo, Cheyenne Mountain Zoo, Jacksonville Zoo, Miami Metrozoo, Milwaukee Zoo, National Park Zoo, Phoenix Zoo, Sacramento Zoo, San Diego Zoo, San Francisco Zoo, and The Zoo.

Samples

Urine was collected from late 1989 until mid-1992. Approximately 1,000 urine samples were collected from the 23 males. Although blood samples may have been preferred for methodological reasons, urine samples have benefits for this type of group comparison study. Urine collection is non-

TABLE 1. Study males

Group	Name	Subspecies	DOB	Secondary sex trait development	Zoo
Juvenile	Mawas	KB	2/89	none	Phoenix
	Duke	KB	8/88	none	Phoenix
	Kiko	PH	11/87	none	National
Arrested adolescent	Jambu	KS	4/85	none	Audubon[a]
	Sinjo	PS	9/83	none	Miami
	Pongo	KH	6/82	none	Brookfield
	Thomas	PH	3/82	none	Milwaukee
	Herbie	PB	4/81	none	Brookfield
	Urban	KS	2/81	none	Sacramento[a]
	Chewy	PS	12/80	none	San Francisco
Developing adolescent	Pumpkin	PB	9/85	occurring	The Zoo
	Tucker	PH	2/83	occurring	National
	Azy	KH	12/77	occurring	National
	Samarinda	KB	6/77	occurring	Cheyenne Mtn.
	Clyde	KS	8/76	occurring	Chaffee
	Geoffrey	PS	11/73	occurring	Jacksonville
Adult	Robin	KH	3/76	complete	Brookfield
	Jasper	KS	3/73	complete	Miami
	Ken	KB	2/71	complete	San Diego
	Dick	KH	1/68	complete	Milwaukee
	Rusty	PS	6/67	complete	San Francisco
	Samu	KB	7/66	complete	Cheyenne Mtn.
	Junior	KH	4/66	complete	National

[a]Housed with aged adult male (>28 years old), data not presented here. PB, probably Bornean; KB, known Bornean; PS, probably Sumatran; KS, known Sumatran; PH, probably hybrid; KH, known hybrid.

invasive and does not cause a stress response, affecting hormone levels, as does blood sample collection. In addition, the time integration effect on urinary hormone levels flattens out transient increases or decreases in blood levels. And last, urinary hormone or hormone metabolite levels and blood hormone levels generally exhibit similar profiles (Monfort et al., 1987; Hourd and Edwards, 1994). Orangutan keepers collected urine from study males at varying frequencies, ranging from whenever possible to two per day. Samples were collected by syringe from the bedroom floor or urinated directly into a cup, labeled with the male's name, the date and time of urine collection, and frozen immediately. Samples were shipped frozen on dry ice to the Center for Reproduction of Endangered Species at the San Diego Zoo (CRES). Each zoo also provided background information for each male including his flange and laryngeal sac developmental status, kinship, housing situation, diet, medical history, growth records (when available), semen quality (when available), and behavioral patterns. Zoos also provided photographs from 1990 and 1992 depicting any gross change in developmental status, as primarily measured by cheek flange and laryngeal sac status.

Hormone assays

Data in this study were derived by use of radioimmunoassay (Abraham, 1975; Yalow, 1992). Each hormone assay used the same urine sample sets. Testosterone radioimmunoassays were conducted in the endocrinology laboratory at CRES. To control for diurnal hormone secretion patterns only samples collected between 7:00 and 10:00 AM were assayed. Testosterone and DHT assays were run on ether extracted, hydrolyzed urine. Urine was hydrolyzed using 0.1 ml of orangutan urine, 0.4 ml pH 5 phosphate buffer, and 0.02 ml glucuronidase-arylsulfatase (Boehringer Mannheim, IN) with incubation in a 37°C water bath overnight. Samples were reconstituted with 1 ml pH 7 phosphate buffer following ether extraction with 5 ml anhydrous diethyl ether. The testosterone assay methodology was developed by Czekala (Robbins and Czekala, 1997). Serial dilutions of orangutan urine samples yielded a parallel dose-response curve to the testosterone standard curve ($r = .985$). Additionally, known amounts of human testosterone added to known orangutan samples were accurately retrieved. Testosterone antibody, tracer, and standards were purchased from ICN Biomedicals, NEN Dupont, and Sigma

Pharmaceuticals, respectively. For testosterone assays: the inter-assay coefficient of variation was 16%; the intra-assay coefficient of variation was 14%; the lowest level of detectability was 3.9 pg/ml; and the cross reactivity was 100% for testosterone, 18.75% for DHT, and less than .01% for cortisol. Levels of creatinine for all urine samples were also measured at CRES, using a Jaffe reaction (Taussky, 1954). All hormone levels are expressed as a ratio to creatinine in order to control for dilution of urine samples.

The gonadotropins and DHT were assessed in the Department of Biological Sciences, Stanford University. All procedures utilized commercially available kits developed for use with human urine, serum, or plasma, but validated for use with orangutan urine. Because of the close relationship between human and orangutan reproductive hormones, these kits cross-reacted with orangutan urine. We were able to show parallel dose-response curves for serial dilutions of orangutan urine and hormone standard curves (for DHT, r = .999; for LH, r = .999; for FSH, r = .996) and accurate retrieval of human hormone added to orangutan samples.

Peptide hormone assays were run on untreated urine, in duplicate, and with two controls. LH and FSH kits were purchased from Pantex (Santa Monica, CA; catalog numbers 017 and 630, respectively). For LH assays: the interassay coefficient of variation was 8%; the intraassay coefficient of variation was 5%; the lowest level of detectability was 0.4 mIU (2 mIU/ml); and the cross reactivity was 100% for LH and less than 1% for FSH, growth hormone (GH), and thyroid stimulating hormone (TSH). For FSH assays: the interassay coefficient of variation was 8%; the intraassay coefficient of variation was 4%; the lowest level of detectability was 0.4 mIU (2 mIU/ml); and the cross reactivity was 100% for FSH and less than 1% for LH, GH, and TSH.

DHT levels were assessed using a kit from Amersham Corporation (Arlington Heights, IL; kit code TRK 600), using the same enzyme-hydrolyzed and ether-extracted urine samples used to evaluate testosterone. Samples were treated with an oxidizing agent and extracted with ether a second time to remove conjugated testosterone as directed by the kit protocol. Assays were run with duplicates and two controls. Due to the cost of this kit, levels were evaluated for only a subset of the original samples. For DHT assays: the interassay coefficient of variation was 2%; the lowest level of detectability was 5 pg/ml; and the cross reactivity was 100% for testosterone (but all testosterone was destroyed by oxidation) and 45–50% for DHT. For DHT assay no intraassay coefficient of variation was obtained, but a two-tailed, paired *t*-test showed that no significant difference between replicates existed.

Data analysis

About one-third of the hormone values obtained were omitted from the analyses for the following reasons. Because the creatinine test, which provides a basis for standardization of urine sample dilution, loses accuracy at about 0.1 mg/ml, samples with low creatinine values were not used in analyses. Samples that may have thawed for an extended period of time were not used in analyses. Samples with values that fell above the range of the standard curve or below the lowest detectable limit of the procedure were omitted. All data were subsequently log-transformed to achieve homoscedasticity and meet the assumptions of analysis of variance (ANOVA). Mean values and standard error of the means were established for each hormone, each animal, and each group using SAS means procedure (PROC MEANS) (Littell et al., 1991). Mean values for each hormone for juvenile, arrested, developing, and adult males were compared by a one-way nested ANOVA and Tukey pairwise comparison test for unbalanced data using SAS general linear models procedure (PROC GLM). ANOVA was also used to detect and control for seasonal secretion patterns for each hormone.

Values in figures are least-square means and standard errors, obtained from an ANOVA of untransformed data, done solely to obtain values for graphing purposes.

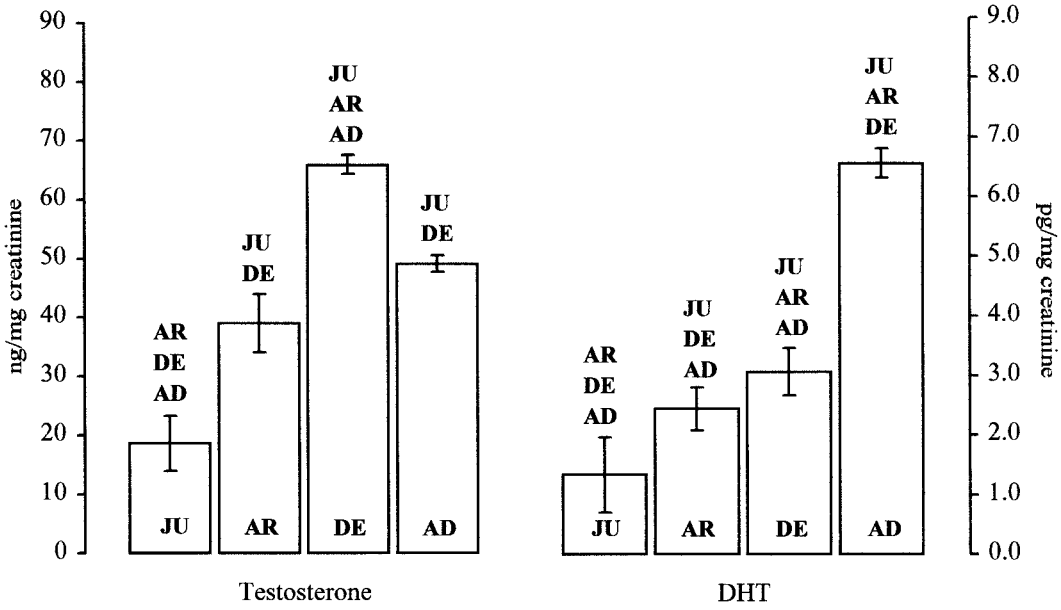

Fig. 1. Testosterone and DHT levels, on different Y axes (least square means and standard errors). JU, juveniles; AR, arrested adolescents; DE, developing adolescents; AD, adults. Letters above bars denote groups which have a significantly different hormone level ($P \leq .02$, unless otherwise noted).

Least-square means represent the group mean of a hormone, holding constant effects due to the time of year and the variation of individuals within each group. These means were recalculated using log-transformed data and compared by the pairwise comparison option (pdiff) in PROC GLM. For the purpose of producing figures using actual units untransformed values were used, however, all comparison statistics were derived using log-transformed data. All tests were judged significant at $P \leq .02$ unless otherwise stated.

RESULTS

Figure 1 illustrates significant differences in testosterone levels between the groups ($F = 37.84$, $df = 4/590$, $P \leq .0001$). Juveniles had testosterone levels significantly lower than any other group (vs. arrested males $P \leq .0001$; vs. developing males $P \leq .0001$; vs. adults $P \leq .0001$). Arrested adolescents had testosterone levels significantly lower than developing adolescents ($P \leq .0001$), but not significantly different from adults. Developing males had significantly higher testosterone levels than all other groups (for all comparisons $P \leq .0001$). Figure 1 also illustrates significant differences in DHT levels between the groups ($F = 62.41$, $df = 4/56$, $P \leq .0001$). Juveniles had the lowest levels of DHT as compared to all other groups (for all comparisons $P \leq .0001$). Arrested males had significantly higher DHT than juveniles ($P \leq .0001$). Developing males had significantly higher DHT than arrested males ($P = .0152$). Adults had significantly higher DHT than developing males ($P \leq .0001$).

Figure 2 illustrates significant differences in LH levels between the groups ($F = 11.24$, $df = 4/266$, $P \leq .0001$). LH was significantly higher in juveniles than all other groups (for all comparisons $P \leq .0001$). It decreased significantly in arrested males ($P \leq .0001$). LH levels were lower in arrested adolescents than developing adolescents ($P = .0620$). LH concentrations were significantly lower in adults than developing males ($P \leq .0001$). Figure 2 illustrates differences in FSH levels between the groups ($F = 10.07$, $df = 4/263$, $P \leq .0001$). FSH levels were similar among juvenile, arrested, and developing adolescent males. FSH concentrations were significantly lower in adults than in develop-

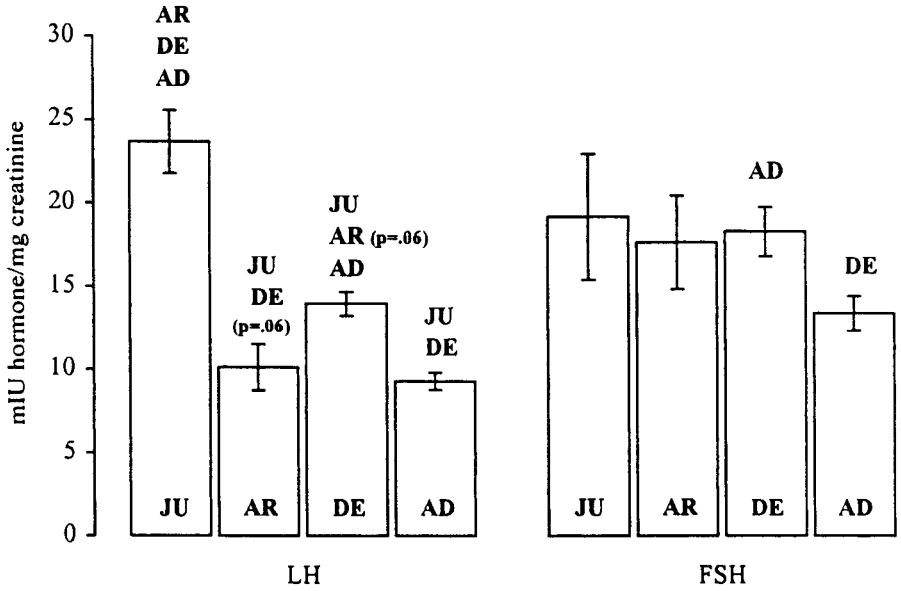

Fig. 2. LH and FSH levels, on same Y axis (least square means and standard errors). JU, juveniles; AR, arrested adolescents; DE, developing adolescents; AD, adults. Letters above bars denote groups which have a significantly different hormone level ($P \leq .02$, unless otherwise noted).

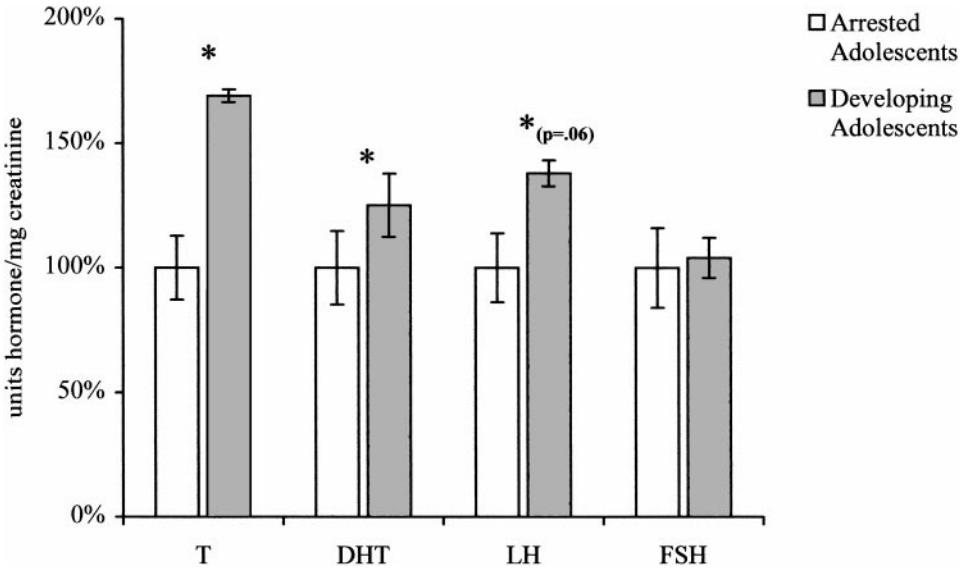

Fig. 3. Summary of hormone levels of adolescent males (arrested = 100%). Asterisk denotes hormone levels which are significantly different ($P \leq .02$, unless otherwise noted). Error bars represent standard errors.

ing adolescents ($P = .0027$). Figure 3 consolidates the results for the four hormones compared between arrested and developing adolescent males (developing male values indexed to arrested male values). Arrested males had lower concentrations of testosterone, DHT, LH than developing males. Arrested and developing adolescents did not

have significantly different concentrations of FSH.

DISCUSSION

Male orangutan endocrine profiles

Each phase of the male orangutan life cycle has a distinct profile for development and reproduction-related hormones. Testicular steroid levels are lowest in juveniles. Arrested adolescent males have testosterone and DHT levels intermediate between those of juveniles and developing males. They have sufficient sex steroids to facilitate primary sexual development and spermatogenesis, but not enough to develop secondary sexual features. Developing males have the highest level of testosterone of the male life cycle and higher DHT than arrested males. Both of these hormones are required for the adolescent growth spurt and development of secondary sexual features. In humans, the highest testosterone level of the male life cycle is mid-adolescence (Janczewski and Bablok, 1985). In adult male orangutans, testosterone level drops below the developing male level, but DHT level is highest for the life cycle. The relationship between testosterone and DHT levels changes between developing adolescents and adults, as has been documented in human males (Schwartz and Bercu, 1992).

Gonadotropin levels are relatively high in juveniles, and this combined with low testosterone and DHT levels suggests that the gonads of male orangutans are relatively insensitive to gonadotropins until puberty. Testicular receptors may be few in numbers or blocked by some other substance. Cortisol and/or prolactin may play a role in making the testes of juveniles insensitive to gonadotropins (Sapolsky, 1985; Norman, 1993; Schwartz and Bercu, 1992). From their analysis of data on gonadotropin levels in juvenile and adolescent chimpanzees, Hobson and colleagues (1991) suggest that gonadotropin levels in juvenile apes prior to puberty may be regulated by an unknown factor of nongonadal origin. They remark that the mechanism controlling gonadotropin secretion during childhood remains obscure (Hobson et al., 1981). However, in a more recent study on puberty in primates, Plant (1994) states that gonadotropin levels are low in juveniles. Because this is not the case in male orangutans, a unique regulatory phenomenon may be occurring. In arrested males, LH level is lower than in developing males. Lower LH concentrations relate to lower testosterone and DHT levels, and lack of enough sex hormone for secondary sexual development. FSH levels of arrested and developing adolescents are similar, such that rates of spermatogenesis and degree of fertility may also be similar. Adults have lower gonadotropin concentrations than developing adolescents reflecting a mature system. During adulthood the hypothalamic-pituitary-gonadal axis functions at its most efficient level and testes are highly sensitive to gonadotropins.

Analysis of testes size in male orangutans also supports that developmentally arrested male orangutans are fertile. Dahl and colleagues (1993) illustrated that subadult males have a higher ratio of testes weight to body weight, .056, as compared to "fully developed" adults, .035. That is, testes become large as early as 7 years of age, well before the adolescent growth spurt and attainment of adult body size. They write that testes development precedes other signs of pubertal development and occurs in males once they reach a threshold weight of about 25 kg. Fully adult size testes have been found in males weighing as little as 34 kg, even though adult body weight for male orangutans is 85–90 kg (Dahl et al., 1993).

In sum, arrested and developing adolescent males have functioning hypothalamic-pituitary-gonadal axes, such that they have higher testosterone and DHT than juveniles. Developing adolescents have higher levels of testosterone, DHT, and LH than arrested adolescents, compatible with secondary sexual trait development. Arrested males do not have adequate concentrations of these hormones to trigger secondary sexual maturation; however, they do have sufficient levels of testosterone and FSH to facilitate spermatogenesis and fertility (Bercovitch and Goy, 1990).

In the only other study of male orangutan developmental endocrinology, Kingsley (1982, 1988) used urine samples to study the gonadal steroids of 20 captive male orangutans ranging from one to 16 years of age.

Kingsley assessed early-morning urine samples for testosterone concentrations by radioimmunoassay and monitored flange growth. Kingsley found that testosterone levels in subadult, "nonflanged" male orangutans were intermediate between juveniles and "flanged" males. While flanges and other secondary sexual features were developing, testosterone concentrations were intermediate between that of "nonflanged" and "flanged" males. Kingsley concluded that the presence of a dominant, "flanged" male suppresses flange growth in subordinate, "nonflanged" males for a period of 2 to 7 years in captivity. Additionally, Kingsley documented siring by captive subadult orangutans (Kingsley, 1982).

A number of factors in Kingsley's study necessitated reassessing testosterone levels in captive males. Since the oldest male orangutan was 16, he may actually represent an older developing adolescent rather than an adult male. In addition, she was unable to measure creatinine levels in some of her samples and used levels of sodium chloride to control for urine dilution. Expressing hormone levels as a ratio to creatinine is the standard method in urinary assay (Czekala et al., 1994; Lasley et al., 1985; Mitchell et al., 1982). In this study we used more study animals from a wider range of ages, collected more urine samples, and used creatinine level to control for urine dilution.

Evolutionary consequences of paired arrest of secondary sexual development and fertility

The fertility of arrested males, despite their absence of secondary sexual features, is of considerable evolutionary significance. Galdikas (1985a,b) has described two reproductive strategies in male orangutans: the "combat/consort" strategy and the "sneak/rape" strategy. The "combat/consort" strategy is generally used by fully mature males and is a high-cost, potentially high-benefit strategy. Subadult or developmentally arrested males typically use the "sneak/rape" strategy. This is a low-cost, low-benefit strategy, according to Galdikas. She states that young males switch from the "sneak/rape" strategy to the "combat/consort" strategy once they start to develop cheek flanges. She also suggests that the two strategies are in balance such that "fitness concerns are ultimately equal" (Galdikas, 1985a).

It is proposed that endocrine data from this study refine these ideas and provide further evidence of an additional developmental pathway and corresponding reproductive strategy in male orangutans. There is a broad spectrum of durations of maturation period in male orangutans, but the two extremes may be the "play it safe" strategy (at puberty become fertile but postpone secondary sexual development) and the "take a chance" strategy (at puberty, rapidly develop primary and secondary sexual features). Both in captivity and the wild, the adolescent maturation process may take as little as a few months or over 10 years (MacKinnon, 1979; te Boekhorst et al., 1990). With the "play it safe" strategy, males minimize aggression and injury from proximate dominant, mature males, while still being able to sire (Kingsley, 1982). And even though females are not attracted to arrested males, forced copulation provides chances for siring. With the "take a chance" strategy, estrous females may be proceptive to males with secondary sexual traits (Galdikas, 1981; Schurmann, 1982; Galdikas, 1985a); however, other mature males may be extremely aggressive, leading to potential injury and stress (Galdikas, 1985a). In orangutans, there is a unique decoupling of time in life of high rate of aggression and time of high rate of reproductive behavior. Subadult males are very sexually active, but rarely involved in male-male aggression, whereas mature males are less sexually active and are very aggressive (MacKinnon, 1979; Mitani 1985a).

Male orangutan developmental patterns and corresponding reproductive strategies may fall on a continuum from rapid, early maturation and potential for high reproductive success due to their access and attractiveness to females, to extended arrest of secondary sexual trait development paired with fertility and reproductive success dependent on forced copulation. It must be that the reproductive success rate of males lacking secondary sexual features is less than that of a males with these features. If this were not the case, expending metabolic

energy to mature would be selected against. However, the difference between the two rates cannot be great, as the alternate pattern of arrested adolescence appears to be maintained by natural selection.

Prepubertal determination of developmental pathway

Anecdotal reports are that young males experience arrested secondary sexual development when housed with dominant, mature males during adolescence (Maple, 1980; Graham and Nadler, 1990). However, the developmental path a male orangutan takes may be determined well before puberty. Wickings and Dixson (1992) found that differences between dominant and subordinate mandrills, where a similar developmental arrest phenomenon occurs, could be detected prior to puberty. In mandrills, prepubescent males with fatted rumps ultimately became social, rapidly developing adolescents, whereas prepubescent males lacking fatted rumps became peripheral, developmentally arrested males. In this orangutan study, being housed with a mature male during puberty did not determine whether or not a growing male developed rapidly or was developmentally arrested. Being housed in the absence of a mature male did correlate with early puberty, as documented by Graham and Nadler (1990), but growing males housed currently with a mature male may or may not be experiencing extended developmental arrest.

Some factor related to juvenile experience may determine the male's developmental and reproductive strategy. Sapolsky and Ray (1989) argue that the differences they see in stress hormone levels in baboons are related to personality types in the animals. Some males deal well with stress and minimize the negative effects of a stress response. These males tend to be dominant. Some males have marked endocrine responses to agonistic encounters and tend to be subordinate. Furthermore, there are two distinct personality types within dominant males; those with the ability to exert social control in male-male interactions, and those who focus energy on developing relationships with females (Ray and Sapolsky, 1992). These personality differences are probably established long before adulthood. Sapolsky and Ray propose that early experiences influence endocrine profiles and dominance relationships in adult male baboons.

The work of Uchida (1996) supports the idea of a prepubertal determination of developmental pathway in male orangutans. She documents the developmental phenomenon occurring in male orangutans using dental and cranial maturation data derived from a museum collection of hunted orangutans. Uchida finds that dental maturation and cranial maturation can be decoupled in orangutans, so that some males who are dentally mature are not yet cranially mature. In young dentally mature males, she finds some with relatively small teeth and some with relatively large teeth. She proposes that large-toothed males may develop quickly, while small-toothed males may experience arrested growth and development. If this is true then whatever occurs to determine the developmental pathway of a male happens prior to dental maturation and puberty.

Growing male orangutans may have evolved a neuroendocrine means of using the long calls of mature males to evaluate their social environment and the density and proximity of their reproductive competitors. The orangutan long call is produced only by mature males and audible to humans up to 800 m away (Mitani, 1990). Mature males produce daily stereotypic long calls both in the wild and in captivity. These calls appear to be important only to male orangutans and have minimal intersexual function; that is, they neither attract nor repel females (Mitani, 1985b). MacKinnon has suggested that subadult males monitor long calls as a means of avoiding adult males (MacKinnon, 1979). Theoretically, an acoustic signal could work like an olfactory signal (pheromone) in arresting development via direct neuronal connections from the auditory area of the brain to the hypothalamus (Vandenbergh, 1994). Perhaps some threshold level of mature male long calls causes decreased secretion of GnRH, interfering with hormones necessary for complete development in growing males (Ronnekleiv and Resko, 1990; Meredith, 1991).

There is some evidence that such auditory socioendocrine phenomenon exist in mam-

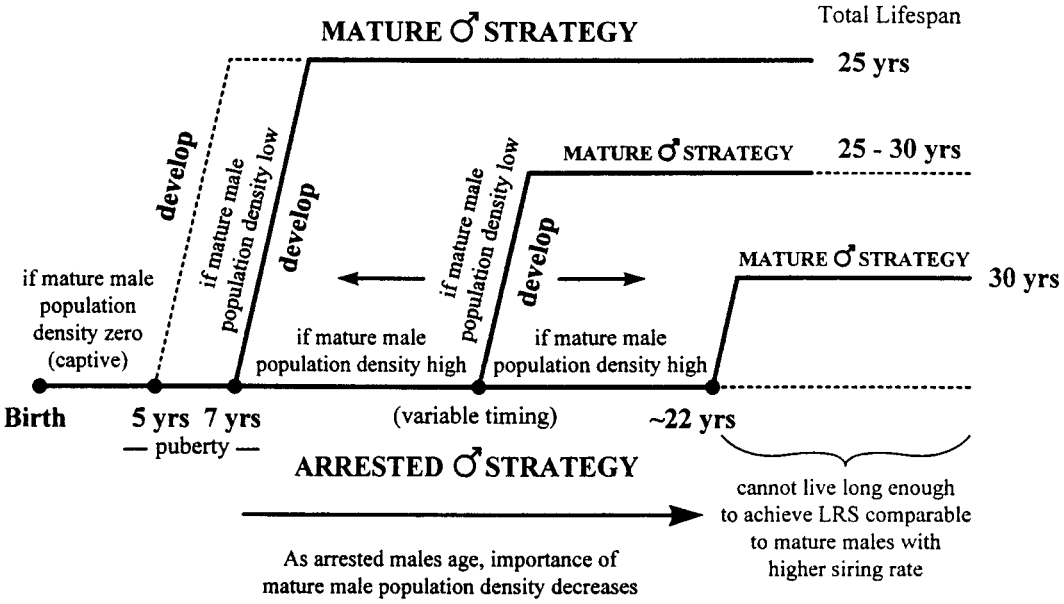

Fig. 4. Decision tree of male orangutan developmental pathways and reproductive strategies. LRS, lifetime reproductive success.

mals (red deer, McComb, 1987). Elowson and Snowdon (1994) have shown that in pygmy marmosets vocal structure changes with a changing social environment and perhaps contains information on many aspects of the current social situation, including population density and level of conflict. Subadult orangutan males may use adult male long calls to monitor their whereabouts and avoid them (MacKinnon, 1979; Mitani, 1985b). Based on the amount of stimulation of this putative neuroendocrine pathway, the young male's endocrinology of growth and development may be altered resulting in an alternative development pathway. The male experiences arrested secondary sexual development, which—coupled with avoidance of mature males and forced copulation with females—allows for reduced agonistic interaction and some reproductive payoff.

Figure 4 is a decision tree of male orangutan developmental pathways and reproductive strategies in which ecological factors and mature male population density play important roles. This decision tree was constructed based on information on two orangutan sites in the wild, Ketambe (Sumatra) as described by te Boekhorst and colleagues (1990) and Tanjung Puting (Borneo) as described by Galdikas (1985a, b, c). At Ketambe, food is more abundant and predictable, and home ranges are smaller than at Tanjung Puting. At Ketambe, the ratio of adult males to adult females is one to three, and the ratio of adult males to subadults is one to two (translating to a one to one ratio of reproductive males to reproductive females). At Tanjung Puting, the adult male to adult female ratio is one to one and subadults are rare. At Ketambe, orangutan population density is high relative to Tanjung Puting.

It is proposed that juvenile males monitor the population density and proximity of mature males. They may do this based on the frequency and intensity of long calls. Based on a socioendocrine interaction between the long calls of mature males and neuronal connections from auditory receptors to the hypothalamus of growing males, the "decision" is made whether to develop rapidly at puberty or to remain more juvenile in appearance. If local mature male density is high, a growing male may "play it safe," becoming fertile but lacking secondary

sexual development. If local mature male population density is low, a growing male may "take a chance," developing rapidly and competing for ranges and females. Ecological factors dictate the density of females in an area, which in turn dictates the density of males, and the density of mature males dictates the developmental and reproductive strategies of growing males.

After puberty, males continue to evaluate mature male density and proximity. If mature male population density decreases, arrested males may develop and switch over to the "take a chance" strategy. If mature male density parameters stay the same, arrested males will remain arrested; however, over time the neuroendocrine effect of long calls on arrested males will decrease as the importance of mature male population density to an individual male's reproductive strategy decreases. Theoretically, at some point the arrested male will develop despite mature male population density, because he will reach an age where it will no longer be possible for him to live long enough to achieve similar lifetime reproductive success (LRS) to males who were never arrested. This assumes that males who never go through an arrested period have a shorter lifespan, due to metabolic costs of development and gonadal steroids, and stress and injury from male-male agonism (McCruden and Stimson, 1991; Dufty, 1989; Ralls et al., 1980; MacKinnon, 1974; Galdikas, 1985a). The upper limit on the male orangutan life span limits the length of time a male can be arrested and necessitates that all males eventually switch from the "play it safe" strategy to the "take a chance" strategy. In captivity, all males appear to eventually develop secondary sexual features, regardless of their social environment.

Thus, a socioendocrine phenomenon may occur in male orangutans, where growing males evaluate the reproductive strategies of their competitors prior to puberty and during any period of arrested secondary sexual development. Then, using this information, a developmental path is determined which minimizes costs related to intrasexual aggression and maximizes reproductive benefits.

CONCLUSIONS

In primate social systems in which one male can monopolize access to reproductive females in an overt manner, other males may evolve an alternative covert strategy for obtaining reproductive opportunities. Selection will favor any male who can somehow circumvent the monopolizing male's ability to control female sexual activity. In the case of the orangutan, it may be that a flexible developmental pathway has evolved whereby some males pair fertility with lack of secondary sexual features. This developmental arrest together with social unobtrusiveness with mature males and forced copulation with females provides subadult males with opportunities to sire.

Orangutans represent the most dramatically dichotomized version of a theme found throughout the primates: that of the covert, lower-metabolic-cost, lower-reproductive-payoff strategy of subordinate males versus the combat-oriented, higher-metabolic-cost, higher-reproductive-payoff strategy of dominant males. However, in orangutans there is a clear-cut morphological underpinning of paired fertility and extended arrest of secondary sexual development. The alternate development and behavioral pattern of subordinate, arrested male orangutans probably does not provide as much reproductive success in the short term as the dominant, mature-male strategy. However, if males who use the alternate strategy can live longer because of avoidance of injury and stress, perhaps the lifetime reproductive success of the alternate reproductive strategies will be similar.

The factor determining which strategy to employ is the male's social environment. Some socioendocrine interaction occurs whereby juvenile males can monitor their social environment. If numerous dominant, mature males exist in close proximity, a male may benefit by using an alternative developmental timeline and corresponding reproductive strategy. If there are few dominant, mature males nearby; however, it may be beneficial to develop quickly and compete for access to estrous females. The result is two types of adolescent male orangutan: one with secondary sexual features and one with-

out. These males have distinct hormonal profiles. The lack of secondary sexual features in arrested adolescent males is commensurate with their lower concentrations of testosterone, DHT, LH compared to developing males. However, there may be no significant difference in fertility levels, as FSH concentrations do not differ between the two types of adolescent male orangutan.

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